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A NEW SPECIES OF PITVIPER OF THE GENUS
TRIMERESURUS (*POPEIA*)
FROM NORTHERN SUMATRA
(REPTILIA, SQUAMATA, VIPERIDAE)

INTRODUCTION

The complex of *Trimeresurus* (*Popeia*) *popeiorum* Smith was revised by VOGEL *et al.* (2004). On the basis of univariate and multivariate analyses, six clusters of populations morphologically diagnosable were recognized. Five of these clusters were considered to be distinct species at the specific level following the Biological Species Concept (BSC) and the Phylogenetic Species Concept (PSC), namely *Trimeresurus* (*Popeia*) *popeiorum* Smith, 1937, *barati* Regenass & Kramer, 1981, *sabahi* Regenass & Kramer, 1981, *nebularis* David, Vogel & Pauwels, 2004 and *fucatus* Vogel, David & Pauwels, 2004. A population from northern Sumatra with 21 dorsal scale rows constituted the sixth cluster but could not be assigned to any species by VOGEL *et al.* (2004). Subsequently, GRISMER *et al.* (2006) described *Popeia buniana* from Pulau Tioman. The reasons why we refer all these species to the subgenus *Popeia* Malhotra & Thorpe, 2004 are explained in the Discussion.

The recent discovery of additional preserved specimens of the Sumatran population not assigned to any taxon by VOGEL *et al.* (2004) allows us to analyse its variation. We consider it to represent a

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full species which is here described. Relationships with other species of the *Trimeresurus (Popeia) popeiorum* complex are discussed, especially the closely related *Trimeresurus (Popeia) sabahi* from Borneo.

MATERIALS AND METHODS

The present paper is based on 6 (2 males and 4 females) preserved specimens of Northern Sumatra and compared with a total of 125 specimens from other parts of the whole range of *Trimeresurus popeiorum*. These specimens were listed in VOGEL *et al.* (2004). We especially compared members of the new species with 10 specimens of *Trimeresurus sabahi* and 17 specimens of *Trimeresurus barati*, which are listed in the Appendix I.

We retained morphological characters used in VOGEL *et al.* (2004). Measurements, except body and tail lengths, were taken with a slide-caliper to the nearest 0.1 mm; all measures on body were taken to the nearest millimetre. Ventral scales were counted according to DOWLING (1951). The terminal scute is excluded from the number of subcaudals. The numbers of dorsal scale rows are given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total number of ventrals) and at one head length before vent respectively. Values for symmetric head characters are given in left/right order. The coloration was observed only on preserved specimens.

A n a l y s e s o f m o r p h o l o g i c a l d a t a

Data of specimens of the *Trimeresurus (Popeia) popeiorum* complex were already analysed by both univariate and multivariate analyses in VOGEL *et al.* (2004). In this latter paper, the population investigated here was identified as Cluster VI. As a consequence we here base the description of the new species only on univariate analyses. The analyses of external morphological data were based on comparisons of statistical values (mean value and standard deviations). Additional data on the pattern of living specimens of Sundaic species were obtained from GUMPRECHT *et al.* (2004) and VOGEL (2006).

A b b r e v i a t i o n s

Morphometry. DEL: distance lower eye margin - edge of the lip. HL: head length. SVL: snout - vent length. TaL: tail length. TL: total length. VED: eye diameter (vertical).

Scalation. C3SL: number of scales between 3rd supralabial and subocular. CEP: cephalic scales (scales on a line between the middle of supraoculars). DSR: dorsal scale rows. MSR: dorsal scale rows at mid-body. VEN: ventral plates. SC: subcaudal plates. SL: supralabial scales.

Statistics. *n*: number of specimens. *x*: mean value. *s*: standard deviation.

Collections. BMNH: The Natural History Museum, London, UK. FMNH: Field Museum of Natural History, Chicago, USA. IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium. MNHN: Muséum National d'Histoire Naturelle, Paris, France. MSNG: Museo Civico di Storia Naturale "G. Doria", Genova, Italy. NHMB: Naturhistorisches Museum, Basel, Switzerland. NHMW: Naturhistorisches Museum Wien, Austria. NMBE: Naturhistorisches Museum Bern, Switzerland. PSGV: Gernot Vogel's private collection, Heidelberg, Germany. RMNH: Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands. USNM: United States National Museum, Washington, USA. ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. ZRC: Zoological Reference Collection, National University of Singapore, Singapore.

RESULTS

In VOGEL *et al.* (2004), specimens from northern Sumatra were included in Cluster VI as defined by multivariate analyses, but at the time the low number of available specimens (2 males, 1 female only) made difficult to ascertain the taxonomic position of this cluster. It was considered close to the cluster of *Trimeresurus sabahi* with which it shares several characters. Here the availability of three additional specimens with 21 dorsal scale rows, bringing the material to a total of 2 males and 4 females allows us to recognize this population as a distinct taxon.

Following the concepts adopted in VOGEL *et al.* (2004) we recognize it at the specific level and describe it as:

***Trimeresurus (Popeia) toba* n. sp.**

(Figs. 1-11)

Lachesis gramineus (nec *Coluber gramineus* Shaw, 1802): BAUMANN 1913: 272.

Trimeresurus cf. *sabahi*: VOGEL *et al.* 2004: 52.

Popeia sabahi (nec *Trimeresurus popeiorum sabahi* Rengenass & Kramer, 1981): SANDERS *et al.* 2006: 355.

H o l o t y p e . MSNG 30988, adult female, from “Si Rambé”, now Sirambi, about 13 km SE of Balige, off the southern shore of Danau Toba (Indonesia, Sumatra Island, Province of Sumatera Utara); collected by Elio Modigliani, 1891.

Paratypes (5 specimens). All from Indonesia, Sumatra Island, Sumatera Utara Province: MSNG 54282 (female), “Pangerang Pisang”, now Pagaran Pisang, a locality on the road between Sibolga and Tarutung, near Adian Koting, leg. Elio Modigliani, 1891; MSNG 54338 (female), “Si Rambé”, now Sirambi, about 13 km SE of Balige, leg. Elio Modigliani, 1891. NMBE 1018072 (210a/198) and NMBE 1018073 (210b/197) (2 males), NMBE 1018074 (210c/199) (female), “Mts. Battak”, at present Batak Mts., Toba Massif.

D i a g n o s i s . A species of the genus *Trimeresurus* Lacépède, 1804, characterized by (1) hemipenes long, reaching in situ at least the 25th SC, without spines; (2) 1st supralabial distinct from nasal; (3) 21 MSR; (4) overall green coloration in males and females without darker crossbands; (5) absence of a postocular streak in both males and females; (6) thin, white ventrolateral stripe present in males, faint but present or absent in females; (7) rather short tail in females with a ratio TaL/TL between 0.148 and 0.157; (8) occipital scales smooth or weakly keeled; and (9) temporal scales large, as large as posterior temporals.

Main characters separating *Trimeresurus* (*Popeia*) *toba* from other taxa of the subgenus *Popeia* are discussed below.

E t y m o l o g y . The specific epithet is the name of the volcanic Toba Massif in which the type locality is located; the same name is applied to the large Lake Toba. It is a noun in apposition.

Suggested English name: Toba pitviper.

D e s c r i p t i o n o f t h e h o l o t y p e (Figs. 1–7). Body elongated, cylindrical; head triangular, wide at its base, thick, rather elongated, clearly distinct from the neck; snout long, accounting for 34.3 % of HL, 2.3 times as long as diameter of eye, flattened, rounded when seen from above, strongly obliquely truncated when seen from lateral side with a very distinct “canthus rostralis”; eye



Figs. 1-2 - *Trimeresurus (Popeia) toba* n. sp. Holotype (MSNG 30988). General view, dorsal (fig. 1) and ventral (fig. 2).



Figs. 3-4 - *Trimeresurus (Popeia) toba* n. sp. Holotype (MSNG 30988). Lateral view of the head, left (fig. 3) and right side (fig. 4).



Figs. 5-6 - *Trimeresurus (Popeia) toba* n. sp. Holotype (MSNG 30988). Dorsal (fig. 5) and ventral (fig. 6) view of the head.



Fig. 7 - *Trimeresurus (Popeia) toba* n. sp. Holotype (MSNG 30988). View of the tail.

large, with VED/DEL ratio 0.7; tail short and tapering, distinctly prehensile.

SVL: 679 mm; TaL: 119 mm; TL: 798 mm; HL: 31.80 mm; ratio TaL/TL: 0.149.

VEN: 155 + 1 lost scale (+ 2 preventrals); SC: 57, paired, plus one terminal scale; anal shield entire.

DSR: 21 – 21 – 15 scales, rhomboid, all nearly smooth.

Rostral visible from above, triangular; nasals subtriangular, undivided, with nostril in their middle; one pair of enlarged, nearly subrectangular and straight internasals, 2.1 times as wide as deep at left, 3.2 times at right, separated by one scale as wide as adjacent upper snout scales; 3 / 3 canthal scales bordering the “canthus ros-

tralis" between the internasal and corresponding supraocular, as wide as adjacent snout scales; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2 / 2 postoculars; 1 entire, long and narrow supraocular on each side, about 2.9 times as long as wide, about 0.8 time as wide as the internasals; supraocular indented on their inner margin by the upper head scales; scales on upper snout surface smooth, juxtaposed, irregular in shape, enlarged, with 6 snout scales on a line between the scale separating the internasals and a line connecting the anterior margins of eyes; cephalic scales small, much irregular, juxtaposed, smooth and flat on upper head surface; 10 CEP in a line between supraoculars; occipital scales flat, smooth; temporals large, as large as or larger than posterior temporals, subequal, in 2 or 3 rows, smooth; one thin, elongated, crescent-like subocular; 10 / 9 SL; 1st SL triangular, short, totally separated from the corresponding nasal; 2nd SL high, forming the anterior border of loreal pit, in contact with nasal; 3rd SL larger than other supralabials, pentagonal, high and long, 1.3 times as long as high, in contact with the subocular; 4th SL short, longer than high, 0.7 time as high as 3rd one, separated from the subocular by 1 large scale; 5th and posterior SL smaller than 4th one, 5th SL separated from the subocular by one scale, others in contact with the first row of temporals; 12 / 12 infralabials, those of the first pair in contact with each other, the first three pairs in contact with the chin shields; 7 / 7 rows of smooth gular scales; chin shields irregularly arranged.

In preservative, the background colour is uniformly deep green, somewhat paler on the lower part of the sides; no ventrolateral stripe.

The tail surface is basically the same colour as the dorsum, barely mottled with faint rusty-brown on near its tip.

The dorsal head surface and temporal regions are of the same colours as the dorsum, slightly more bluish-green above and on the temporal regions, paler green on the supralabials; no postocular streak. Eyes are yellowish-orange.

The venter and throat are uniformly yellowish green, lighter than the back.

To our best knowledge, this species has never been depicted or even described alive.

Description of the paratypes (Figs. 8–11) and variation. All characters of paratypes agree well with those of the holotype, with the variation below explained.

Body more slender in males and somewhat thicker than in females; triangular head average in length, amounting for 4.7–6.0 % of SVL, wide at its base, flattened in males, rather thick in females when seen from the side. Snout long, elongated and strongly obliquely truncated when seen from the side, amounting for 23.7–36.6 % of HL or 1.8–3.6 times as long as diameter of eye, with a very distinct “canthus rostralis”. Eye large, amounting for 0.7–1.2 ($x = 1.0$) times the distance eye–lip. Tail long in males, rather short in females and prehensile. Ratio TaL/TL: 0.149–0.230, with a strong sexual dimorphism (see below).

DSR: 21–24 – 21 – 15–16, distinctly keeled in males, weakly keeled or smooth in females, always smooth on the 1st DSR.

VEN: 153–156 (plus 1–2 preventrals); SC: 57–73, all paired; anal shield entire.

Internasals separated by either 1 scale (in 4/6 specimens) or 2 scales (2/6 specimens); 3–5 canthal scales between the internasal and corresponding supraocular, slightly larger than adjacent snout scales, bordering the “canthus rostralis”; 2 small postoculars; one entire supraocular on each side, long and rather narrow, 2.3–3.4 ($x = 2.8$) times as long as wide, 0.60–1.20 ($x = 1.00$) times as wide as the internasals; 5–6 scales on the snout on a line between the scale(s) separating the internasals and a line connecting the anterior margins of the eyes; 10–12 ($x = 10.8$, $s = 0.8$) cephalic scales on a line between supraoculars, smooth and flat; occipital scales larger than cephalic scales, smooth or a few weakly keeled in both sexes; temporals large, smooth and in 3 rows; 9–10 SL (9–9: 1/6 specimens; 9–10: 1/6; 10–10: 4/6); 1st SL short and separated from nasal; 2nd SL forming the anterior border of loreal pit, separated from nasal by 0–2 scales; 3rd SL largest, longer than high, in contact with the subocular (6/12 occurrences) or separated by 1 scale (6/12); 4th SL longer than high, shorter than 3rd SL, separated from subocular by 1 scale in all specimens on both sides; 5th SL separated from subocular by 1 (8/12 occurrences) or 2 small scales (4/12) large scales; 10–13 IL ($x = 11.8$, $s = 1.0$), those of the first pair in contact with each other, and first three pairs in contact with anterior chin shields; 7–8 rows of smooth gular scales; throat shields irregularly arranged.



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Figs. 8-9 - *Trimeresurus (Popeia) toba* n. sp. Paratype (MSNG 54282). General view, dorsal (fig. 8) and ventral (fig. 9).



Figs. 10-11 - *Trimeresurus (Popeia) toba* n. sp. Paratype (MSNG 54338). General view, dorsal (fig. 10) and ventral (fig. 11).

In preservative, the background colour is uniformly deep green. In the two available males and in 2 out of 4 females, a thin white ventrolateral stripe extends from the neck, fainter in females.

The tail surface is basically the same colour as the dorsum, faintly mottled with rusty-brown on its sides and below, entirely reddish-brown in its most posterior part; under surface of the tail paler than above.

The dorsal head surface and temporal regions are of the same colours as the dorsum, paler green on the supralabials. In both males and females, the postocular streak is absent. Eyes golden or yellow.

The venter and throat are uniformly light green or yellowish green, lighter than the back.

Main morphological characters of the holotype and paratypes are summarized in Table 1.

Tab. 1 - Main morphological characters of the type specimens of *Trimeresurus (Popeia) toba* n. sp. (See Materials & Methods for the abbreviations).

Collection number	NMBE 1018072	NMBE 1018073	NMBE 1018074	MSNG 30988	MSNG 54282	MSNG 54338
Sex	♂	♂	♀	♀	♀	♀
SVL (mm)	562	430	284	679	364	299
TaL (mm)	168	118	53	119	65	55
TaL / TL	0.230	0.215	0.157	0.149	0.152	0.155
PosOc streak	none	none	none	none	none	none
Lateral stripe	white	white	none	none	faint	faint
VEN	155	153	153	155 (+1 lost)	154	156
SC	73	73	58	57	64	59
SL	9 / 9	10 / 10	10 / 10	10 / 9	10 / 10	10 / 10
CEP	10	11	11	10	12	11
C3SL	0 / 0	1 / 0	1 / 1	0 / 0	0 / 1	1 / 1

The maximal known total length is 798 mm (SVL 679 mm, TaL 119 mm) for a female (MSNG 30988, holotype). The largest known male is 730 mm long (SVL 562 mm, TaL 168 mm; NMBE 1018 072).

S e x u a l d i m o r p h i s m . Although our sample is limited, a strong dimorphism appears in:

(1) the ratio TaL/TL: males: 0.215–0.230 ($\bar{x}$ = 0.223, s = 0.01); females: 0.149–0.157 ($\bar{x}$ = 0.153);

(2) differences in the number of subcaudals: 73 in our two males vs. 57–64 ($\bar{x}$ = 59.5) in females.

There is no difference in the numbers of ventral scales or, more interestingly, in the pattern. According to our material, females may have or lack the white ventrolateral stripes present in males.

D e s c r i p t i o n o f t h e h e m i p e n e s . From NMBE 1018072 (in situ): hemipenes are bilobed, smooth, long and slender, and reach the 25th SC.

R a n g e . Indonesia. Known only from Sumatra Island: Sumatera Utara Province (or North Sumatra Province), in the southern part of Toba Massif.

This volcanic massif is the result of a massive volcanic eruption that occurred only 75,000 years ago. Its slopes are partly covered with montane forests.

C o m p a r i s o n w i t h o t h e r s p e c i e s . *Trimeresurus* (*Popeia*) *toba* n. sp. differs from the other taxon of the subgenus *Popeia* present on Sumatra, *Trimeresurus* (*Popeia*) *barati* Regenass & Kramer, 1981, by (1) 21 MSR vs. 19 (rarely 17) MSR in *T. barati*; (2) a bicolour ventrolateral stripe, reddish-brown below / white above, in *T. barati*, white only in both sexes of *T. toba*; and (3) a longer tail in females of *T. barati*, 0.164–0.176 vs. 0.149–0.157 in *T. toba*.

Trimeresurus (*Popeia*) *toba* n. sp. differs from *Trimeresurus* (*Popeia*) *popeiorum* Smith, 1937 by the following characters: (1) no postocular streak in males and females vs. a conspicuous bicolour postocular streak in males and a thin white postocular streak in females of *T. popeiorum*; (2) a thin white ventrolateral stripe in males vs. a vivid wide bicolour (red or orange + white) ventrolateral stripe in *T. popeiorum*; (3) a thin white ventrolateral stripe in females of *T. popeiorum*, which is absent or faint in females of *T. toba*; (4) tail

brown, laterally mottled with green in *T. popeiorum* vs. mottled only towards its tip in *T. toba* and (5) in the nearly unkeeled occipital scales and temporal scales (distinctly keeled in *T. popeiorum*).

Trimeresurus (Popeia) toba n. sp. differs from *Trimeresurus (Popeia) fucatus* Vogel, David & Pauwels, 2004 by (1) the lower relative tail length of the females (0.149–0.157 vs. 0.159–0.189 in *T. fucatus*); (2) the lower number of ventrals in males (153–155, $\bar{x}$ = 154.0 vs. 156–171, $\bar{x}$ = 164.0 in *T. fucatus*); (3) the lower number of ventrals in females (153–156, $\bar{x}$ = 154.5 vs. 157–170, $\bar{x}$ = 163.4 in *T. fucatus*); (4) the nearly unkeeled occipital scales and temporal scales vs. distinctly keeled in *T. fucatus*; (5) the absence of a red ventrolateral stripe in males. Furthermore it differs from the northern populations of *T. fucatus* in the absence of dark crossbands and a vertebral row of white dots, and a tail that is mottled only towards its tip where it is mottled throughout in northern populations of *T. fucatus*.

Trimeresurus (Popeia) toba n. sp. is much similar to *Trimeresurus (Popeia) nebularis* Vogel, David & Pauwels, 2004, known from the Cameron Highlands of West Malaysia and South Thailand. Both taxa share a uniform pattern, absent postocular streaks, and reduced or absent ventrolateral stripes. They differ by (1) a higher number of ventrals in *T. toba* n. sp., 153–156 vs. 147–153; (2) a shorter tail in females of *T. toba* n. sp.: ratio TaL/TL 0.149–0.157 vs. 0.165–0.172; (3) tail dark rusty brown above, green laterally with a sharp border between the colours in *T. nebularis* vs. faintly mottled in *T. toba* n. sp.; (4) and eye green in *T. nebularis* vs. yellowish-orange in *T. toba* n. sp. according to our preserved material.

Lastly, *Trimeresurus (Popeia) toba* n. sp. is also quite similar to *Trimeresurus (Popeia) sabahi* Regenass & Kramer, 1981 endemic to Borneo Island. Both species can be separated by (1) bicour ventrolateral stripes in males, white and well defined in females of *T. sabahi*, reduced to thin white lines in males of *T. toba* n. sp., present or absent in females; (2) sides of tail green, widely mottled with rusty brown, with a sharp border between the colours in *T. sabahi*, indistinctly mottled at the exception of the tail tip in *T. toba* n. sp.; (3) tail longer in females of *T. sabahi* with a ratio TaL/TL of 0.173–0.178 vs. 0.149–0.157 in *T. toba* n. sp.; (4) eye deep red or bright orange in *T. sabahi*, yellowish-orange in *T. toba* n. sp.. Both species share a postocular streak absent in males and females, occipital and

temporal scales smooth or weakly keeled and other main scalation characters.

DISCUSSION

Generic position. Based on combined morphological and molecular analyses, MALHOTRA & THORPE (2004) showed that the genus *Trimeresurus* “sensu Auctorum” contained five major clades which were assigned to seven genera. Species of the *popeiorum*-complex were referred to the new genus *Popeia*. This position has been adopted by most authors. However, we consider that recognizing either a genus *Trimeresurus* or a genus *Popeia* are acceptable on a phylogenetic basis; both schemes have positive and negative points. If one considers *Trimeresurus* as a single genus, the information on the phylogenetic relationships among the various clades within the genus *Trimeresurus* is lost but the monophyly of the main clade *Trimeresurus* is emphasized in regards of other Asian (*Ovophis* Burger, 1981 and *Tropidolaemus* Wagler, 1830) and American pitviper genera. It is the reverse if one considers valid the seven genera defined by MALHOTRA & THORPE (2004). In this latter case, one should better consider a “super-genus” *Trimeresurus*. As a consequence, we recognize the distinct taxonomic status of these clades but we consider them to be better considered to be subgenera in a well defined genus *Trimeresurus*. It should also be noted that, on a morphological basis, these genera are hardly diagnosable.

Taxonomic status. Before VOGEL *et al.* (2004), no specimen of *Trimeresurus toba* n. sp. seem to have been discussed in the literature at the exception of BAUMANN (1913). These specimens had not been examined by REGENASS & KRAMER (1981) and were not included in the account of *Trimeresurus popeiorum barati* in DAVID & VOGEL (1996) or mentioned by GUMPRECHT *et al.* (2004). However, specimens of the NMBE museum were included in the morphological analyses of SANDERS *et al.* (2006) (see below).

Trimeresurus toba n. sp. is here described for one of the two populations of the subgenus *Popeia* currently known from Sumatra. The other one, inhabiting western Sumatra (Padang Highlands, Mt. Kerinci), was assigned to *Trimeresurus barati*, a rather homogeneous taxon, by VOGEL *et al.* (2004). This latter taxon differs in having only 17 or 19 MSR.

VOGEL *et al.* (2004) could not conclude about the taxonomic position of the populations of Toba Massif due to availability of only three specimens. They were tentatively regarded as related to the Bornean *Trimeresurus sabahi*, with which they share most characters, as explained above.

A point to be discussed is the taxonomic position of *Trimeresurus (Popeia) toba*. One possible position would be to recognize it as a subspecies of *Trimeresurus (Popeia) sabahi* Regenass & Kramer, 1981. Here, we adopt the same position than in VOGEL *et al.* (2004), namely the Phylogenetic Species Concept (PSC) for allopatric populations.

The recognized species are fully diagnosable by the combination of a low number of morphological characters and fall into the basic definition of the PSC. This point was discussed at length in VOGEL *et al.* (2004), to which we refer. All recognized species of the subgenus *Popeia* of the Sunda Region share major morphological characters such as a low number of ventral scales, lack of postocular streak in both sexes, a uniform dorsal pattern, and so on, but at same time show constant morphological differences of their own and are clearly diagnosable.

These Sundaic taxa occur in mountains of the Sunda Region and seem to have similar ecological requirements. As explained in VOGEL *et al.* (2004), the palaeobiogeography of the Sunda Region suggests that these now isolated populations are remnants of a former widespread equatorial species. During the Pleistocene period of the Quaternary (about 1.6M–17.000 years BP), the world climate was affected by alternating periods of cooling and heating, with associated dry and wet periods in the tropical regions. Higher parts of the Sunda Shelf, namely the mountain ranges on the margin of this basin which now constitute the current ranges of West Malaysia (Cameron Highlands), Sumatra (Barisan Range and the Toba Massif) and Borneo (Mt. Kina Balu, Crocker Range, and so on) were not as much affected and constituted suitable refuges. The populations have since remained isolated each from the others. A summary of the distribution of species of the subgenus *Popeia* in these mountains may be found in VOGEL *et al.* (2004).

R e l a t i o n s h i p s . On the basis of morphological characters, VOGEL *et al.* (2004) recognized two main groups within the subgenus

Popeia. The first one includes *Trimeresurus popeiorum* and *Trimeresurus fucatus*. Both species are characterized by a high number of ventral scales, usually strongly keeled occipital and temporal scales, at least in males, and the presence of a postocular streak. The second group is characterized by a low number of ventral scales, usually smooth occipital scales and smooth temporal scales, and the absence of a postocular streak in males; it includes four species of the Sunda Region inhabiting highlands of West Malaysia, Borneo and Sumatra respectively. *Trimeresurus toba* belongs to this latter group.

On the basis of morphological and mt-DNA phylogeny, SANDERS *et al.* (2006) proposed a different interpretation. *Trimeresurus (Popeia) popeiorum* and *Trimeresurus (Popeia) nebularis* were considered to be distinct lineages deserving a specific status in agreement with VOGEL *et al.* (2004). However, in contrast to VOGEL *et al.* (2004), SANDERS *et al.* (2006) considered all other lineages from Southern Thailand, West Malaysia and the Sunda Shelf (including North Sumatra) to belong to a single species for which the specific combination *Popeia sabahi* was selected. We consider that gathering all these taxa in a single species is not in agreement with both morphological variation, biology of the populations (mountain forms as *T. sabahi*, *T. barati* and *T. toba* were grouped together with lowland forms as *T. fucatus* and *T. bunianus*), and the biogeography of Southeast Asia. As explained above, we have little doubt on the fact that *Trimeresurus sabahi*, *T. barati* and *T. toba* belongs to the same clade, possibly along with *Trimeresurus bunianus* according to GRISMER *et al.* (2006), but *Trimeresurus fucatus* should be excluded from this lineage. Future studies will confirm its status.

Quite interestingly, the PCA plot of SANDERS *et al.* (2006) place the male NMBE specimens of *Trimeresurus (Popeia) toba* next to specimens from Borneo, an interpretation confirmed by our own data.

Key. The seven recognized species of the subgenus *Popeia* may be separated each from the others only by combinations of characters. This key updates the one given by VOGEL *et al.* (2004). Data on *Trimeresurus (Popeia) bunianus* are derived from GRISMER *et al.* (2006). A greater emphasis is put on characters of the pattern, often the easiest way to differentiate species of this group.

- 1 17 or 19 MSR, endemic to West Sumatra and Mentawai Islands *Trimeresurus barati*
- 21 (rarely 20) MSR 2
- 2 Postocular streak usually present in males and bicolour (red + white), also possibly present in females as a thin white line; occipital and temporal scales strongly keeled at least in males; usually equal or more than 158 ventrals 3
- Postocular streak always absent in both sexes; occipital and temporal scales smooth or weakly keeled even in males; less than 158 ventrals 5
- 3 Eyes deep red; no crossbands on the body; a conspicuous bicolour postocular streak in males, often a white postocular streak in females; sides of the base of the tail widely green; ratio TaL/TL 0.18–0.21 in males, 0.15–0.175 in females; not known South of the Isthmus of Kra
. *Trimeresurus popeiorum*
- Eyes not bright red; dark reddish-brown crossbands on the body in males; a thin postocular streak, either bicolour or not; sides of the base of the tail with little or no green; present South of the Isthmus of Kra 4
- 4 Eyes greenish-yellow, gold or yellow copper; reddish-brown dorsal crossbands, present also in females; numerous and conspicuous white vertebral dots in males, often present in females; a thin, conspicuous or faint bicolor postocular streak may be present in males, sometimes absent, often absent or reduced to a thin streak or dots in females; ratio TaL/TL 0.19–0.24 in males, 0.16–0.19 in females; 156–171 VEN; known only from the mainland
. *Trimeresurus fucatus*
- Eyes turquoise with a maroon centre; purplish-brown dorsal crossbands, strongly contrasted in males, absent in females; no white dots on the body; a broad, maroon postocular streak in males, no streak in females; ratio TaL/TL 0.22–0.23 in males, 0.22 in females; 170–174 VEN; known only from Pulau Tioman
. *Trimeresurus bunianus*

- 5
- Eye green; tail rusty brown above, green laterally, with a sharp border between the two colours; less than 66 SC in males; no red ventrolateral stripe in males; endemic to West Malaysia *Trimeresurus nebularis*
-
- Eye orange or yellow or gold; tail more or less mottled with rusty brown and green; more than 68 SC in males; red ventrolateral stripe possible in males; not present in West Malaysia 6
- 6
- Bicolour ventrolateral stripe in males, white and well defined in females; eyes deep red or bright orange; sides of tail green, widely mottled with rusty brown, with a sharp border between the colours; ratio TaL/TL in females 0.173–0.178; endemic to Borneo
. *Trimeresurus sabahi*
-
- Ventrolateral stripe as a thin white line in both sexes or absent in females; eyes yellowish-orange; sides of tail indistinctly mottled at the exception of the tail tip; ratio TaL/TL in females 0.149–0.157; endemic to northern Sumatra *Trimeresurus toba* n. sp.

CONCLUSION

The description of *Trimeresurus toba* raises to 11 the number of pitvipers known from Sumatra and adjacent islands: *Ovophis monticola convictus* (Stoliczka, 1870), *Trimeresurus* (*Trimeresurus*) *andalasensis* David, Vogel, Vijayakumar & Vidal, 2006, *Trimeresurus* (*Trimeresurus*) *brongersmai* Hoge, 1969, *Trimeresurus* (*Trimeresurus*) *puniceus* (Boie, 1827), *Trimeresurus* (*Cryptelytrops*) *albolabris* (Gray, 1842), *Trimeresurus* (*Cryptelytrops*) *purpureomaculatus* (Gray, 1832), *Trimeresurus* (*Parias*) *hageni* (Lidth de Jeude, 1886), *Trimeresurus* (*Parias*) *sumatranus* Raffles, 1822), *Trimeresurus* (*Popeia*) *barati* Regenass & Kramer, 1981, *Trimeresurus* (*Popeia*) *toba* n. sp., and *Tropidolaemus wagleri* (Boie, 1827) (see DAVID & VOGEL 1996; VOGEL *et al.* 2004; DAVID *et al.* 2006). To this list should be added another potential species identified as *Trimeresurus* cf. *puniceus* by DAVID *et al.* (2006), and *Calloselasma rhodostoma* (Boie, 1827), the occurrence of which in Sumatra has never been confirmed.

The scheme of the repartition of the *popeiorum*-complex on Sumatra matches the one observed in the *puniceus*-complex, namely in each case a northern taxon, *Trimeresurus toba* n. sp. and *Trimeresurus andalasensis*, which in both cases is quite distinct from taxa occurring in the Barisan range, namely *Trimeresurus puniceus* and possibly *Trimeresurus* cf. *puniceus*, and *Trimeresurus barati*. Quite interestingly, in both groups the North Sumatran species is morphologically closer to a species occurring on Borneo, *Trimeresurus borneensis* (Peters, 1872) and *Trimeresurus sabahi* respectively. The collecting of additional Sumatran specimens of pitvipers of the subgenus *Popeia* is necessary to ascertain the biogeographical relationships of this complex in the various mountain ranges of the island and of the Sunda shelf.

APPENDIX

Specimens examined. Only specimens of the taxa occurring in the Sunda Region are listed here. Others were listed in VOGEL *et al.* (2004).

***Trimeresurus (Popeia) barati* Regenass & Kramer, 1981**

Indonesia, Sumatra Island.

BMNH 1915.12.2.42 (male), "Sungei Kumbang, Korinchi, Sumatra", a stream on slopes of Mt. Kerinci, Sumatera Barat Province.

NHMB 2587 (male, holotype), Solok, Sumatera Barat Province.

SMF 21226 (male), Bungur, Riau Province.

NHMW 23910:1, NHMW 23910:3 (females), NHMW 23910:2 (male), "Pagay, Sumatra", one of Pagai Islands, Mentawai Archipelago, Sumatera Barat Province.

NHMW 23917:1–23917:6, NHMW 23917:8–23917:9 (all males), NHMW 23917:7, NHMW 23917:10 (females), Padang, Sumatera Barat Province.

RMNH 17190A (female), Padang, Sumatera Barat Province.

Trimeresurus (Popeia) nebularis Vogel, David & Pauwels, 2004
Federation of Malaysia, West Malaysia.

IRSNB 2627 (male), Cameron Highlands (4°29'N–101°23'E), State of Pahang.

MNHN 2004.0501, ZRC 2.2887 (males), PSGV 626, ZRC 2.2884–85 (females), Cameron Highlands, State of Pahang.

USNM 142425, adult female, from Gunung Brinchang [now Gunung Batu Berinchang], Cameron Highlands, State of Pahang.

ZFMK 82856, Gunung Batu Berinchang, Cameron Highlands, State of Pahang.

Trimeresurus (Popeia) sabati Regenass & Kramer, 1981

Federation of Malaysia, Borneo Island.

BMNH 96.4.29.10 (male), “Saiap, Kina Balu”, now Sayap, Gunung Kinabalu, State of Sabah.

FMNH 233155, FMNH 243942 (females), Sipitang District, State of Sabah.

FMNH 251048 (male), Tambunan District, State of Sabah.

MNHN 1889.220–221 (males), “Mont Kinabalu”, State of Sabah.

RMNH 8241 (male), “Borneo, voet van de Simedoen” [foot of the Simedoen], now Mt. Semedoem (1118 m asl), a mountain feeding Sungei Landak, a tributary which falls into Kapoeas River at 00°01'S–109°21'E, at a short distance from Pontianak, State of Sarawak.

USNM 130253 (male), Bundu Tuhan, Mt. Kinabalu, State of Sabah.

USNM 134128 (female), Tenompok, Mt. Kinabalu, State of Sabah.

ZFMK 51767 (male), Headquarters, Mt. Kinabalu, 1500 m asl, State of Sabah.

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ABSTRACT

A new species of pitviper of the genus *Trimeresurus* (*Popeia*) from Northern Sumatra (Reptilia, Squamata, Viperidae).

The discovery of additional specimens of a population of Sumatran pitvipers previously identified as *Trimeresurus* cf. *sabahi* allows a reinvestigation of its status. This population from northern Sumatra is here referred to a new species, *Trimeresurus* (*Popeia*) *toba* n. sp. which differs from other species of the *Trimeresurus* (*Popeia*) *popeiorum* complex, and especially those of the Sunda Region, by a combination of morphological characters in scalation and color pattern.

This new taxon seems closer to *Trimeresurus sabahi* from Borneo but is regarded as a distinct species following the Phylogenetic Species Concept. The island of Sumatra is inhabited by two species of the *Trimeresurus* (*Popeia*) *popeiorum* complex, *Trimeresurus* (*Popeia*) *barati* from western Sumatra and the Mentawai Archipelago (with 17 or 19 dorsal scale rows) and *Trimeresurus* (*Popeia*) *toba* n. sp. (with 21 dorsal scale rows) from northern Sumatra. This distributional pattern is quite similar to that observed in the complex of *Trimeresurus puniceus*. An updated key to the *Trimeresurus* (*Popeia*) *popeiorum* complex is provided.

RIASSUNTO

Una nuova specie di crotalino del genere *Trimeresurus* (*Popeia*) di Sumatra settentrionale (Reptilia, Squamata, Viperidae).

La scoperta di alcuni esemplari di una popolazione di trimeresuri di Sumatra, precedentemente identificati come *Trimeresurus* cf. *sabahi*, ha permesso un approfondimento dello status di questa popolazione che viene attribuita a una nuova specie, *Trimeresurus* (*Popeia*) *toba* n. sp., che differisce dalle altre del complesso di *Trimeresurus* (*Popeia*) *popeiorum*, specialmente da quelle della Regione della Sonda, per una combinazione di caratteri morfologici nel numero e nella disposizione delle squame e nella colorazione.

Questa nuova entità sembra vicina a *Trimeresurus sabahi* di Borneo ma viene considerata distinta seguendo il concetto filogenetico di specie. L'isola di Sumatra è abitata da due specie del complesso di *Trimeresurus* (*Popeia*) *popeiorum* e in particolare *T. barati* di Sumatra occidentale e dell'Arcipelago delle Mentawai (con 17 o 19 file di squame dorsali) e *T. toba* n. sp. (con 21 file di squame dorsali) di Sumatra settentrionale; lo schema della distribuzione è abbastanza simile a quello osservato nel complesso di *Trimeresurus puniceus*. Viene fornita una chiave dicotomica aggiornata per il complesso di *Trimeresurus* (*Popeia*) *popeiorum*.